

## Convergent Evolution in Western North American and Patagonian Skippers (Hesperiidae)

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**Abstract.** The western North American skippers *Polites sabuleti* and *Pyrgus scriptura*, typically found in saline or alkaline semiarid habitats, are phenotypically remarkably similar to *Hylephila zapala* and *Pyrgus seminigra* from similar habitats in Argentine Patagonia. Their behavior is effectively identical, and the two *Pyrgus* deviate behaviorally from their close relatives. The host plants of *P. sabuleti* and *H. zapala* are identical; those of the two *Pyrgus* are subspecies or sister-species. Placement in distinct genera makes *P. sabuleti* and *H. zapala* unambiguously convergent. Phylogenetic relationships within *Pyrgus* are unclear, but *P. scriptura* and *P. seminigra* appear to belong to different, allopatric species-groups or lineages and to have evolved their similarities by parallelism or convergence.

*The shape of a crystal is determined solely by the molecular forces, and it is not surprising that dissimilar substances should sometimes assume the same form: but with organic beings we should bear in mind that the form of each depends on an infinitude of complex reactions...It is incredible that the descendants of two organisms, which had originally differed in a marked manner, should ever afterward converge so closely as to lead to a near approach to identity throughout their whole organization.*

—Charles Darwin, *On the Origin of Species* (1859)

Darwin objected not to the reality of convergent evolution, with which he was thoroughly familiar, but to the idea that it could progress so far that competent systematists would be unable to distinguish convergence from homology (resemblance due to common ancestry). Yet debates of this sort continue to enliven the zoological literature. Biochemical-genetic methods (Sibley and Ahlquist 1987) have resolved some of them. A good example of the problem is the striking similarity of much of the high-Andean and Patagonian butterfly fauna to that of the temperate and boreal Holarctic (Descimon 1986). Although historical-biogeographic scenarios deriving the Andean fauna from the Holarctic have been current for nearly a century, the matter is still unresolved for most taxa (Shapiro 1991). Paradoxically, the greatest ambiguity lies at relatively high taxonomic levels (genera and above). When individual *species* show remarkable similarity but demonstrably belong to different lineages and cannot be each other's closest relatives, a diagnosis of convergence is assured. This is especially true when the resemblance extends to behavior and ecology, implying adaptive significance rather than the effects of

mere chance. Thus there is great uncertainty as to whether the Andean *Yramea* is closely related to the Holarctic *Boloria*, but no doubt that the uncanny phenotypic similarity of an undescribed oreal *Yramea* from northwestern Argentina to the boreal *Boloria improba* Butler is convergent.

Among such species-level convergences, a few spectacular cases have been described which strain the biologist's credulity. Cody (1974, pp. 165-168) summarizes a number of avian examples, including the near-legendary American meadowlark *Sturnella* (Icteridae) and African pipit *Macronyx* (Motacillidae) which fooled Linnaeus, and which are still virtually indistinguishable even as hand specimens (Friedmann 1946). Using a picture book such as Lewis (1973), it is possible to synthesize numerous cases of seemingly striking convergence in butterflies, but without behavioral and ecological information they are not very credible.

In the course of field work in temperate North and South America, I have twice been struck by apparent convergence equivalent to the *Sturnella-Macronyx* case. Both instances involve Hesperidae. Perhaps unsurprisingly, the South American taxa are obscure and poorly documented. Both cases involve saline or alkaline, semiarid habitats. Although the two North American species are frequently sympatric (especially in California), their Patagonian equivalents occur in similar habitats but widely separated from each other. In both cases my initial encounter with the Patagonian species elicited a shock of recognition — equivalent to encountering an old friend in a very unlikely place.

### ***Polites sabuleti* and *Hylephila zapala***

*Polites sabuleti* Bdv. (type locality "California"), the Sandhill Skipper, is fairly widespread in western North America (fig. 1), breaking into a bewildering array of subspecies and local races in the Sierra Nevada and Great Basin. The nominate, lowland Californian subspecies occurs primarily in saline or alkaline seeps or on sand with a high water table, where its native host, the perennial grass *Distichlis spicata* (L.) Greene, is commonly the aspect dominant. Other consistent plant associates are semisucculent Chenopodiaceae. The life history of *P. sabuleti* was briefly described by Comstock (1929).

The genus *Polites* is wholly Nearctic.

*Hylephila zapala* was described by Evans (1955, pp. 313-314) from a pair collected at Zapala in the Province of Neuquén by P. Köhler and forwarded by K. Hayward. Evans identifies these with Hayward's figures (1951, pl. IV and XVI) of *Hylephila bouletti* Mab. This same pair had earlier been called *H. peruana* Draudt by Hayward (1934, pp. 111-112), which he corrected to *bouletti* a few years later (1941, p. 287) (*peruana* is considered a Peruvian subspecies of *bouletti*). In Hayward's final catalogue (1973) he used the name *zapala* and gave its range as "Neuquén (and) Chubut." The true *bouletti* is also listed from far to the north in Catamarca, following Evans. This usage is nearly correct. A member of

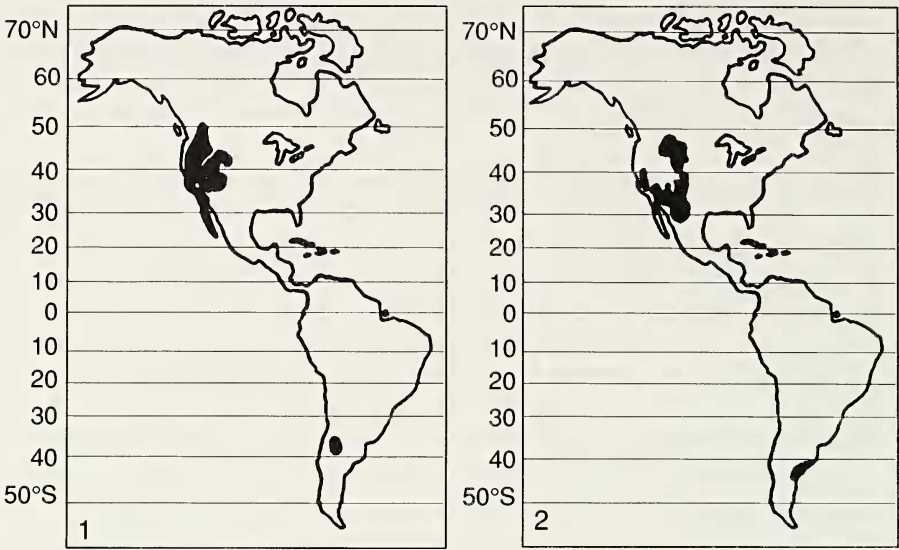


Fig. 1. Distribution of *Polites sabuleti* (all subspecies) in North America, from Scott 1986, and of *Hylephila zapala* in South America.

Fig. 2. Distribution of *Pyrgus scriptura* in North America, from Scott, 1986, and of *P. seminigra* in South America.

the *bouletti* complex, probably undescribed, occurs at high elevation in the Cumbres Calchaquíes and Sierra de Aconquija, a very high pre-Andean range in Tucumán and Catamarca. The rather dissimilar *H. isonira mima* Evans, also listed by Hayward (1973) from Catamarca, occurs below it in the same ranges (also in Salta and in the *cordillera Real* in San Juan). I have not found any Chubut specimens of *H. zapala*, but the habitat is common enough there.

The currently documented range of *H. zapala* is thus contained within Neuquén, from Chos Malal (866m) in the far north to Zapala (1012m) in the central part of the Province. It is locally common in marshy alkaline seeps in high desert, localities inevitably dominated by *Distichlis spicata* and various *Chenopodiaceae*. It does not occur in cooler, moister, less saline inundated meadows (*mallines*) farther west, as at Loncopué (892m), where it is replaced by the mesic-Patagonian and Chilean *H. signata* Blanch. and *H. fasciolata* Blanch. *H. zapala* is at least double-brooded (November and January).

Fig. 3A, B shows habitats of Californian *P. sabuleti*: 3C, D Patagonian *H. zapala*.

Hesperiine skippers are often confusingly similar, but fig. 4A, B demonstrates that *P. sabuleti* and *H. zapala* transcend the ordinary. The detailed resemblance extends to the individual spots forming the complex pattern of the ventral hindwing beneath. These species are much more similar in pattern than are most montane races of *P. sabuleti* to the

lowland California phenotypes. Naive observers presented with the two species have consistently noted the more prolonged apex of the *Hylephila* forewing, as well as differences in the shape of the male stigma and occasionally the shorter antenna in *Hylephila*.

No detailed description of the behavior of *P. sabuleti* has been published. Scott (1986, p. 444) states that "Males perch all day in low grassy spots to await females," a more or less generic description of skipper epigamic behavior. The mating behavior of *Hylephila phyleus* Drury has been described thoroughly by I. Shapiro (1975, 1977). This, the only North American *Hylephila*, sometimes co-occurs with *P. sabuleti* and is useful as a comparison with it and its own congener, *H. zapala*. Although *H. phyleus* will breed on *Distichlis*, it is neither restricted to it nor particularly common in saline areas and alkali seeps. Unlike *P. sabuleti*, it is not effectively restricted to perching on *Distichlis* turf or nearby bare soil. All three species are perchers, but *H. phyleus* males often select roosts several cm above ground level, on projecting vegetation or litter; *H. zapala*, like *P. sabuleti*, consistently perches on the ground (>100 observations of each). Both *H. zapala* and *P. sabuleti* oviposit singly on the undersides of *Distichlis* blades, flying between bouts. *H. zapala* has not been reared.

### ***Pyrgus scriptura* and *P. seminigra***

*Pyrgus scriptura* Bdv. (type locality "California"), the Least Checkered Skipper, is indeed the smallest Pyrgine skipper in North America and rivals the African and Middle Eastern species of *Spialia* for global honors. Although its range is fairly extensive (fig. 2), throughout this range it is local and rarely taken far from its host plant. Only two hosts, both Malvaceae, are recorded: *Sphaeralcea coccinea* (Pursh) Rydb. in Colorado (Ferris and Brown 1980) and *Malvella leprosa* ssp. *hederacea* Torr. (= *Sida hederacea* (Dougl.) Torr.) in California. These two plants are not closely related but are very similar in habit, both being low, spreading, perennial and pubescent. The life history of *P. scriptura* remains unpublished, although it has been reared many times. Minno (1981) studied its bionomics; Dusheck (1984), its host plant relations. Dusheck describes its habitat in California as "the drying borders of alkaline marshes in the Sacramento and San Joaquin Valleys, as well as vacant lots and railroad tracks," and of *M. leprosa* ssp. *hederacea* as "heavy compacted...clay soils...more or less moist saline areas below 1800m." She found that females would not oviposit on other (non-pubescent) mallows in the laboratory, but larvae were easily reared on them. Whatever the eco-evolutionary basis for monophagy in the field, it is neither toxicity nor nutritional inadequacy of the unused mallow species.

*Pyrgus seminigra* was described by Hayward (1933, p. 273 and pl. XXIX, mistakenly cited in the text as pl. XXIV) as a "form" of what he called *Erynnis emma* Stgr., differing from the typical in lacking the marginal row of light spots and the white discal dot on the hindwing

above. The figured specimen indeed presents a solidly black hindwing above. Second-brood specimens are darker than first, but nearly all I have seen do have at least traces of the discal dot. The habitat is given as Chubut and the south of the Province of Buenos Aires.

By 1941 Hayward called it *Pyrgus bocchoris* Hew. form *seminigra*, with no additional data; likewise Hayward 1948. Evans (1953, p. 216) treats *seminigra* as a junior synonym of *P. bocchoris* ssp. *cuzcona* Draudt, type locality Cusco, Peru. Like Hayward (1941), he treats *emma* as a junior synonym of *bocchoris*. Hayward (1973) follows Evans on all points, listing *bocchoris* from the northern, high-Andean Provinces of La Rioja, Catamarca and Tucumán and *seminigra* from La Rioja, Tucumán and Jujuy — without mentioning the southern records in the original description! Evidently his concept of his own taxon had changed.

MacNeill (pers. comm.) treats *seminigra* as a subspecies of *cuzcona*, which he separates from *bocchoris*. All of these entities are very similar in facies and in genitalia. Some specimens of the common, weedy Chilean subspecies of *bocchoris*, *tresignatus* Mab., are nearly indistinguishable from Patagonian *seminigra*, though they average significantly larger. I have elected to treat *seminigra* as a species in this paper, given the uncertainties in its affinities and especially its geographic isolation in northeastern Patagonia. This is an extraordinary disjunction from the southern Peruvian highlands, not duplicated in any other organism known to me. Moreover, temperate seasonality has been a very difficult barrier for tropical high-Andean butterflies to overcome (Shapiro 1991). It is also difficult to construct a scenario that would put *seminigra* where it is and nominate *bocchoris* in the high Andes of northwestern Argentina, between it and *cuzcona*, if these two are indeed more closely related to each other than either is to *bocchoris*.

The ranges of *Pyrgus scriptura* and *P. seminigra* are given in fig. 2.

*Seminigra* is abundant in eastern Chubut (Trelew, Puerto Madryn, Rawson, Uzcudún), north to the vicinity of Viedma and Carmen de Patagones. It seems always to occur with the very widespread, but less common *Pyrgus fides* Evans. (Typically, the taxonomy of this entity is also confused. Hayward, 1933 first figured it as *tresignatus* and recorded it from the Sierras of Córdoba (P. Kohler). In 1941 he corrected the name to *fides* and gave records from Córdoba, Mendoza, Neuquén, Río Negro and San Luis, repeating all of this in 1973. Evans (1953) correctly placed *tresignatus* as the lowland Chilean subspecies of *bocchoris*: it is not known from Argentina).

*Pyrgus seminigra* is restricted to alkaline seeps, mostly on compacted clay soils, floristically and physiognomically equivalent to *P. scriptura* habitats in California (fig. 3, A, B vs. E, F). It is confined to the immediate vicinity of its only known host, *Malvella* (= *Sida*) *leprosa* (Ortega) Krapov. This plant is apparently identical to Californian *hederacea* except in flower color (cream in *hederacea*, sulphur yellow in *leprosa*). It ranges from "Mexico to Patagonia, in saline soils" (Cabrera 1953, p. 310), often

very widely disjunctly. These two plants, now placed in *Malvella* Jaub. & Spach., have no very close relatives in the Americas. Like *P. scriptura*, *P. seminigra* often occurs on waste ground, along railroad tracks, and in very degraded or abused sites.

As in the *Polites-Hylephila* case, many checkered skippers are phenotypically similar, and the *Pyrgus* pattern is very conservative. However, these two species (fig. 4C, D) are the smallest and darkest in their respective faunas, and the same pattern elements tend toward obsolescence in each. Their resemblance is not, however, especially close on the ventral hindwing. What attracts attention in this pair, however, is not so much their phenotypes as their behavior and ecology.

Scott (1986, p. 495) says of *P. scriptura*: "Males patrol and sometimes perch all day in swales or gullies to seek females." Minno (1981) contrasts the behavior of *scriptura* with sympatric *Pyrgus communis* Grote: "*Pyrgus communis*...patrol by flying between six and twelve inches (15-30 cm) off the ground, stopping frequently to feed and occasionally to bask. *Pyrgus scriptura* assumes a somewhat different patrolling style in that males fly closer to the ground and land frequently on vegetation or bare soil to bask." This comparison is quite accurate. *P. scriptura* seldom fly >10 cm above the ground. They never engage in the nearly circular reconnoitering flights characteristic of *P. communis*. While the flight of *communis* is fast and direct, *scriptura* appears almost indolent when not alarmed, flying with a zigzag, skipping motion which is reminiscent of a small Bombyliid (Diptera). The flight of *P. scriptura* is most exaggerated in the small, late summer broods.

The flight and behavior of *P. seminigra* resemble those of *scriptura* closely, contrasting analogously with the much stronger flight and higher perching of sympatric *fides*. Males of the two Patagonian species are easily distinguished, but ovipositing females may not be. *Pyrgus fides* breeds on a variety of Malvaceae, including weedy naturalized *Malva* ssp., erect annual *Sida* (in Neuquén and Mendoza), and *M. leprosa*. *Seminigra*, like *scriptura*, appears strictly monophagous afield. Chilean *bocchoris* are associated with weedy mallows, but remarkably the life history is unpublished.

The eggs of *P. seminigra*, like those of *P. scriptura*, are laid singly on the under surfaces of mature leaves. *P. communis* will lay eggs almost anywhere on a host. *P. fides* is not well-known.

Although Emmel and Emmel (1973) remark that *P. scriptura* occurs "sparingly" in the Colorado and Mojave deserts of southern California and is "never taken in large numbers," this is not true in the California Central Valley. There, it is one of three abundant butterflies in its unusual habitat, *P. sabuleti* and *Brephidium exilis* Bdv. (Lycaenidae) being the others. In eastern Chubut, *P. seminigra* is likewise abundant. The phenomenon of high population densities in species of low-diversity faunas, so-called "density compensation," was first described for islands (MacArthur, Diamond and Karr 1972). In skippers it often results in

suppression of territorial perching behavior, as described by Shapiro 1970, p. 120. Such is effectively the case here.

## Discussion

*Phylogenetic Considerations.* *Hylephila* is an Andean genus, reaching the highest altitudes of any Hesperine skippers in the Americas. The weedy lowland species *H. phyleus* probably entered North America in the Great American Interchange or thereafter (i.e., within the past 3 MY), and its range expanded to its climatic limits with the introduction of the weedy grass *Cynodon dactylon* (L.) Pers. It now ranges from New York City and northern California to extreme northern Patagonia. MacNeill and Herrera are currently revising the genus. There is no basis available to reconstruct the phylogenetic relationships among species, except to say that *H. zapala* does not appear to be a primitive member of the genus, especially close to the genus *Polites*, or the sister-species of *P. sabuleti*. Ergo, its resemblance to *P. sabuleti* must constitute convergence.

Although *Pyrgus* is desperately in need of global revision and offers unusually interesting opportunities for phylogenetic reconstruction, no such project seems to be in progress. Early subdivisions of *Pyrgus* were based on the male secondary sexual characteristics, which, however, appear extraordinarily labile albeit not within species. On genitalic as well as biogeographic grounds, *P. seminigra* belongs to an Andean cluster of taxa. *P. scriptura* is somewhat aberrant but seems most closely related not to the Andean *Pyrgus* but to *P. ruralis* Bdv. (male costal fold present) and *P. xanthus* Edw. (absent, as in *scriptura*). The reduced patterns of both species are derivative in their lineages, and the derivative character of *P. scriptura* is underscored by its seasonal dimorphism, the spring phenotype being virtually identical to the single phenotype of *P. xanthus*. Thus, *P. scriptura* and *P. seminigra* cannot be sister-species.

*Host Relations.* I can find no record of the hosts of *P. cuzcona* or nominate *P. bocchoris* (or of Chilean *trisignatus*, though it is known to eat Malvaceae). There are plenty of mallows in the high-Andean flora up to 4500m (Halloy 1983 discusses an extreme case). The hosts of high-Andean *P. bocchoris* are probably species of *Nototriche* or *Malvastrum*. *P. fides* is also a mallow feeder. Thus all of the Argentine Andean and Patagonian *Pyrgus* investigated so far are mallow feeders. In western North America, both *P. ruralis* and *P. xanthus* feed on herbaceous perennial Rosaceae. The Rosaceae-Malvaceae duality is pronounced in the swarm of sibling species of this lineage in Europe, some of which feed on one, some on the other, and one (*P. malvae* L.) perhaps on both (Higgins and Riley 1970). Mallow feeding has presumably arisen several times in the Holarctic *Pyrgus*, and is derivative within its lineage in *P. scriptura*.

All *Hylephila* and *Polites* are presumably grass feeders. *Distichlis* occurs naturally on both continents. It is the most common oviposition substrate of all of the Andean and Patagonian *Hylephila* I have studied

from Arequipa, Peru south. It may well be the ancestral host of the genus. In *Polites*, turfgrasses are not usual substrates; only *sabuleti* and its desert races feed on *Distichlis*. The montane races feed mainly on bunchgrasses such as *Festuca idahoensis* Elmer. One may thus infer that *P. sabuleti* has diverged more from its relatives in its host relations than has *H. zapala*.

*"Parallelism" and Convergence.* Traditionally, evolutionary biologists and systematists have distinguished between these two terms, depending on the degree of relationship between the taxa. Simpson (1961) defined parallelism as "the development of similar characters separately in two or more lineages of common ancestry and on the basis of, or channeled by, characteristics of that ancestry." The repeated "discovery" of Malvaceae in the Holarctic *Pyrgus* described above, would be a typical case. Eldredge and Cracraft (1980) argue against the concept on grounds of parsimony and intrinsic ambiguity; it is operationally unfeasible to demonstrate a homologous genetic basis for allegedly parallel traits except by hybridization experiments (which are ruled out in cases of full speciation). Shapiro (1986) showed by such experiments that seasonal polyphenism was developed in genetically non-homologous ways by two members of the same polytypic species. If this may occur, it is dangerous to make assumptions about genetic homology at all. I therefore treat the resemblances between *Pyrgus scriptura* and *P. seminigra* as convergent.

*Historical Biogeography.* If we are not dealing with disjunctions between sister-taxa, it is not necessary to "account" for the geographic relationships shown in figs. 1 and 2. There are in fact floristic affinities between western North America and the Patagonian region. The best-known are those between the Sonoran desert and the Argentine *monte* (Solbrig *et al.* 1977); the taxa described here do not properly pertain to these biota. *Pyrgus* is almost certainly a Holarctic element in the Andean Fauna, but the diversity of the genus in South America argues against it being as recent there as the Great American Interchange.

*Determinism and "Adaptive Syndromes."* Both situations described here represent apparently integrated syndromes or suites of characters, including morphology, wing pattern, behavior, habitat and host plant. Is any single factor the trigger for the development of such syndromes? The two *Pyrgus* discussed here are very similar to the various species of the Old World genus *Spialia*, found in arid and semiarid (occasionally mesic)

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(Overlay) Fig. 3. Habitats of western North American and Patagonian skippers. A, B, habitats of both *Polites sabuleti* and *Pyrgus scriptura* in spring, Solano County, central California, with *Distichlis spicata* and *Malvella leprosa* ssp. *hederacea*. V, 1979. C, habitat of *Hylephila zapala* at Chos Malal, Neuquén. I.1981. D, probable type locality of *H. zapala*, Zapala, Neuquén, I.1981. E, habitat of *Pyrgus seminigra*, Trelew, Chubut. The shrubs are naturalized *Tamarix*. XII.1989. F, same site as E showing large clone of *Malvella leprosa* ssp. *leprosa* growing intermixed with *Atriplex hastata*. *P. seminigra* was very abundant here. XII.1989. All photos by AMS.





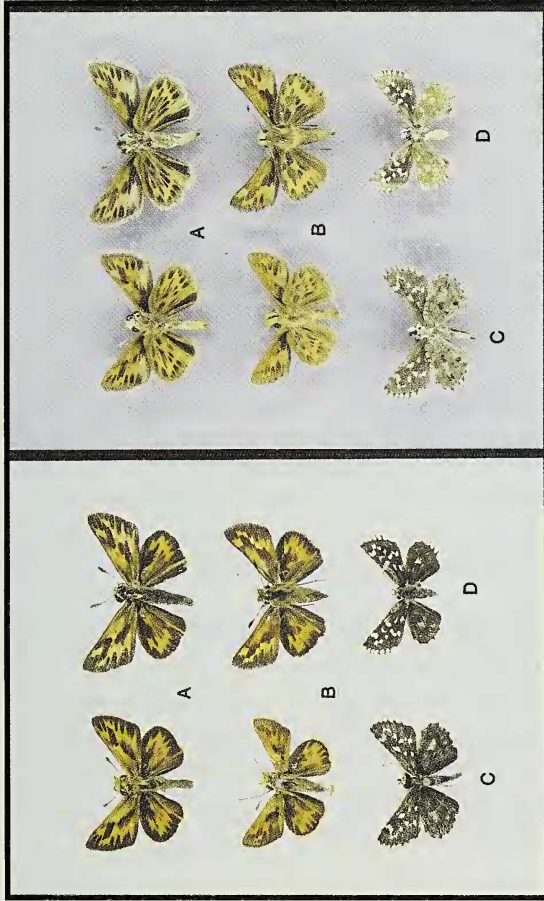


Fig. 4. Dorsal and ventral surfaces of convergent skippers. A, Male and female *Hylephila zapala*, Chos Malal, Neuquén, Argentina, I.1986. B, male and female *Polites sabuleti*, West Sacramento, Yolo Co., Calif., VI.1981. C, Male *Pyrgus seminigra*, Trelew, Chubut, Argentina, XII.1989. D, Female *Pyrgus scriptura*, Suisun Marsh, Solano Co., Calif., IX.1974. Photos by S.W. Woo.

habitats in southern Europe, Africa, and the Near East. All species of *Spialia* are confusingly similar among themselves, and indeed may be indistinguishable on the wing. Their behavior, as described in various regional works, is also very similar. However, their host plants are taxonomically diverse, embracing Convolvulaceae, Sterculiaceae, Malvaceae and Roseaceae (Larsen 1974, Larsen and Larsen 1980). Thus the identity of the host cannot be the determining factor (unless speciation and host-plant specialization have occurred too recently for much phenotypic differentiation to have occurred). Yet, as noted above, *Pyrgus scriptura* uses two phenotypically similar, but not closely related, mallows not used by other *Pyrgus* and growing in unusual habitats. Clearly some kind of determinism is operating, but it is maddening when such elusive selection factors seem able to produce remarkably precise, detailed resemblances.

The most definitive study of convergence in a functional context is by Mares (1980). Every biology student learns that widespread convergence has occurred in the morphology of desert granivorous mammals, embracing not only various rodent groups but members of other lineages, even marsupials, as well. Mares examined entire faunas using quantitative morphometrics and was able to demonstrate convincingly that morphology was correlated with, and presumably functional in, feeding ecology.

The principal barrier to such sophisticated methods being brought to bear on, say skippers is the lack of an ecological data base. The checkered skippers appear ideally suited to such treatment, combined with a rigorous phylogenetic analysis - but there is not even any anecdotal literature on the biology of most of the species, and even common North American and European species have never had their life-histories published.

Cody (1974) points out that structurally simple habitats seem to produce a high frequency of convergence. The occurrence of two striking cases of convergence in different skipper subfamilies in precisely the same, simple community in two hemispheres, as reported here, hardly seems accidental. While not all alkaline seeps in temperate North and South America have any skippers, there seem to be remarkably few ways to be a skipper there at all.

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